PERGAMON

Vision Research 41 (2001) 1423–1435

Vision Research

www.elsevier.com/locate/visres

Integrating electrophysiology and neuroimaging of spatial selective attention to simple isolated visual stimuli

G.R. Mangun [a,*], H. Hinrichs [b], M. Scholz [b], H.W. Mueller-Gaertner [c,d], H. Herzog [c], B.J. Krause [c,d], L. Tellman [e], L. Kemna [e], H.J. Heinze [b]

[a] *Center for Cognitive Neuroscience, Duke University, Box 90999, Durham, NC 27708, USA*
[b] *Department of Clinical Neurophysiology, University of Magdeburg, Magdeburg, Germany*
[c] *Department of Nuclear Medicine (KME), Research Center Juelich, Germany*
[d] *Department of Nuclear Medicine, Heinrich-Heine-University, Duesseldorf, Germany*
[e] *Institute of Medicine (IME), Research Center Juelich, Germany*

Received 2 November 2000; received in revised form 1 February 2001

Abstract

Visual-spatial attention involves modulations of activity in human visual cortex as indexed by electrophysiological and functional neuroimaging measures. Prior studies investigating the time course and functional anatomy of spatial attention mechanisms in visual cortex have used higher-order discrimination tasks with complex stimuli (e.g. symbol matching in bilateral stimulus arrays, or letter discrimination), or simple detection tasks but in the presence of complex distracting information (e.g. luminance detection with superimposed symbols as distractors). Here we tested the hypothesis that short-latency modulations of incoming sensory signals in extrastriate visual cortex reflect an early spatially specific attentional mechanism. We sought evidence of attentional modulations of sensory input processing for simple, isolated stimuli requiring only an elementary discrimination (i.e. size discrimination). As in prior studies using complex symbols, we observed attention-related changes in regional cerebral blood flow in extrastriate visual cortex that were associated with changes in event-related potentials at a specific latency range. These findings support the idea that early in cortical processing, spatially-specific attentional selection mechanisms can modulate incoming sensory signals based on their spatial location and perhaps independently of higher-order stimulus form.

Keywords: Electrophysiology; Neuroimaging; Visual-spatial attention

1. Introduction

Selective attention to events in the visual world involves changes in sensory–neural processing independent of the direction of gaze. These influences of *covert* attention can alter stimulus processing at latencies that suggest a modulatory influence of attention on *input processing*, as shown by recordings of event-related potentials (ERPs) in humans (e.g. Van Voorhis & Hillyard, 1977; see Mangun, 1995 for a review). Single neuron recordings in monkeys have supported the time course of information derived from ERPs, and have permitted attention effects on sensory processing to be localized to specific neuroanatomical stages of the visual system (e.g. Moran & Desimone, 1985; see Luck, Chelazzi, Hillyard, & Desimone, 1997 for a review). In humans, the neuroanatomy of visual attention effects on sensory processing has been investigated using functional neuroimaging using positron emission tomography (PET) (e.g. Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Heinze et al., 1994). More recent studies have helped to relate attentional modulations of sensory processing to specific, functionally-defined visual areas using functional magnetic resonance imaging (fMRI) (e.g. Tootell et al., 1998; Martinez et al., 1999; see Kanwisher & Wojciulik, 2000 for a review), thereby providing a common neuroanatomical link between the animal work at the cellular level and research in humans. However, neuroimaging studies alone do not

* Corresponding author.
E-mail address: mangun@duke.edu (G.R. Mangun).

0042-6989/01/$ - see front matter
PII: S0042-6989(01)00046-3

provide evidence about the time course of identified neural activity with attention, and therefore additional evidence must be gathered in order to relate neuroimaging work to electrophysiological studies in humans or animals.

In prior studies, we developed a method to investigate the time course and functional anatomy of visual-spatial selective attention in humans using a combined electrophysiological and neuroimaging approach (Heinze et al., 1994; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Mangun, Buonocore, Girelli, & Jha, 1998). In those studies we demonstrated that extrastriate visual areas were modulated by selective spatial attention (based on PET and fMRI), and that these regions were active at short post-stimulus latencies (based on ERP recordings). For example, in our initial work in this area we showed that activity in the posterior fusiform gyrus in visual cortex was the likely generator of ERP attention effects in the P1 latency range (70–130 ms after stimulus onset). We did this in a task in which subjects were required to discriminate complex nonsense symbols at attended locations in the visual field while ignoring simultaneously presented stimuli at other locations. Based on these data, and those in follow-up studies (Mangun et al., 1997, 1998) we argued that the spatially-defined modulation of incoming sensory signals could act as a gain control mechanism over perceptual processing, and that this occurred in the extrastriate cortex in regions consistent with visual areas V2 through V4, a conclusion consistent with subsequent imaging findings (e.g. Vandenberghe et al., 1996; Vandenberghe et al., 1997; Woldorff et al., 1997; Martinez et al., 1999) and with studies in animals (e.g. Luck et al., 1997; McAdams & Maunsell, 1999; Reynolds, Chelazzi, & Desimone, 1999). Other studies have extended this work to demonstrate that under some conditions, attentional modulations in humans and animals may occur in V1 (e.g. Motter, 1993; Somers, Dale, Seiffert, & Tootell, 1999; for a review see Sengpiel & Huebener, 1999), and perhaps earlier in the lateral geniculate nucleus of the thalamus (Vanduffel, Tootell, & Orban, 2000). This effect of selective spatial attention can be likened to an attentional 'spotlight' that relatively facilitates stimuli falling within the attended zone of the visual field while attenuating stimulus processing for events outside the attended region.

In the present study we extent our prior work (e.g. Heinze et al., 1994; Mangun et al., 1997, 1998) into visual spatial attention using the combined ERP and PET approach. We addressed three key questions about the nature of the attentional modulations observed in prior combined ERP and neuroimaging studies of spatial attention. First, although prior findings were consistent with the idea that spatial attention modulates input processing in extrastriate cortex as a function of spatial location, the *complex symbol stimuli* used in earlier studies left open the possibility that activations in visual cortex were actually related to higher-level perceptual processes applied to stimuli falling within the spotlight of attention. As a result, even though corresponding ERP evidence argued for modulations of input processing based on spatial location, the PET (and fMRI) activations with attention might have been related to other forms of attentional processing of visual inputs, such as those based on form cues. Similar concerns are also relevant to other studies in the literature that have investigated spatial attention using complex, higher-order stimuli such as letters (e.g. Martinez et al., 1999;Somers et al., 1999; Martínez et al., (2001)). Here we test this by using simple vertical grating stimuli that should not activate specialized, higher-order form analyses processes that might, in principle, have been activated by the complex symbols used previously (e.g. Heinze et al., 1994; Mangun et al., 1997).

Not all evidence of modulations of visual cortex with spatial attention in studies combining ERPs and neuroimaging have used complex stimuli, however. Woldorff et al. (1997) used checkerboard stimuli with a luminance detection task and observed correlated ERP and neuroimaging effects related to spatial attention in the extrastriate cortex. Woldorff et al. found only weak activation in posterior fusiform cortex in ventral occipital lobe, finding the strongest activations in dorsal occipital areas. They interpreted these differences from prior studies as the result of variations in the locations of their stimuli in the visual field in comparison to earlier studies, in line with the retinotopic organization of visual cortex (e.g. Tootell et al., 1998; Brefczynski & DeYoe, 1999). Although this is an intuitively pleasing interpretation, no direct tests of this proposal were made for combined ERP and PET data. Here we use approximately the same stimulus locations that we have used in several prior studies (e.g. Heinze et al., 1994; Mangun et al., 1997, 1998 — upper visual field lateralized stimuli) but simplify the stimuli and the requirements of the subjects' task (although the attentional load of the task was maintained at a high level by making the discrimination difficult). Other studies using neuroimaging methods alone have also used relatively simple stimuli and tasks (e.g. Tootell et al.), but these studies have not incorporated high-resolution time course information, and therefore whether any given neural activation observed reflects input gating awaits convergent information (c.f. Martinez et al., 1999).

Second, in addition to the complexity of the stimuli employed previously, *the task of symbol-matching* used in some studies may also have invoked higher-order perceptual comparisons processes that produced activations in visual cortex. Such processes might reflect activity that was not related to modulations of input processing based on spatial location alone. For example, in our prior studies (Heinze et al., 1994; Mangun et

al., 1997, 1998) we required subjects to discriminate the two nonsense symbols at the attended location and determine whether they were the same or different. Such a complex perceptual task required, by definition, that the stimuli were extensively processed before the same/different judgment could be made. Reafferent attention-related activations of early stages of visual cortical processing might well be involved in such a task, while not actually representing changes in input processing per se. Whether or not such a mechanism might have led to the activations in lingual and fusiform gyrus that we and others (e.g. Martinez et al., 1999) have observed previously, remains unclear. Thus, in the present study we employ a task that involves more simple size judgments (height discrimination) to minimize the possibility that any attention-related modulations observed in visual cortex in our prior reports might have resulted from relatively later comparison processes invoked to perform tasks such as complex symbol matching.

Finally, in our earlier imaging studies we presented stimuli in bilateral arrays. Thus, attended-location stimuli were placed in competition with unattended-location events. It has been argued that under these conditions, selective modulation of stimulus inputs may occur earlier in sensory analyses than if no such competition between targets and distractors must be resolved (e.g. Motter, 1993; Worden & Schneider 1996; see also, Desimone & Duncan, 1995; Tootell et al., 1998; Brefczynski & DeYoe, 1999; Kastner & Ungerleider, 2000). However, in numerous ERP studies using single, isolated stimuli presented sequentially to attended and ignored locations, short-latency modulations of visual processing have been observed (e.g. Eason, 1981; Mangun & Hillyard, 1991; Luck et al., 1994; Handy & Mangun, 2000), and even when the stimuli are presented at a relatively slow rate (Mangun & Buck, 1998). To test whether the activations we have reported in ventral visual cortex are dependent on there being competition between attended and ignored stimuli, in the present study we presented the stimuli one at a time in a rapid sequence to the attended and ignored locations.

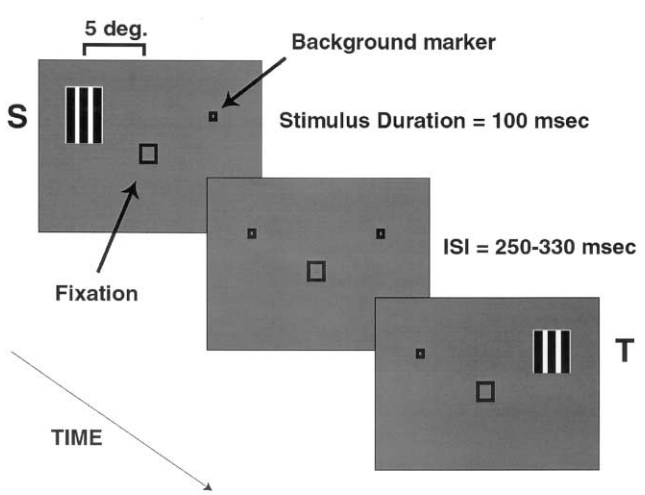

Fig. 1. Stimulus arrays and timing. Stimuli consisted of vertically oriented gratings presented on a gray background that were rapidly flashed in a random sequence to left and right upper field locations. See text for details.

The study presented here tests the conditions under which covert visual-spatial selective attention influences input processing in visual cortex. The study specifically investigates whether modulations of early visual cortical areas in humans will be observed when attention is directed to simple, isolated stimuli requiring only elementary judgements. ERP and PET measures of visual processing were obtained in separate sessions from the same group of subjects while they performed a spatial attention task. The task required them to maintain fixation on a central point while covertly attending either a right or left field location, or passively viewing the stimuli (in separate blocks). Simple grating stimuli were presented in isolation to the left and right field locations in a fast stimulus stream. The subjects made a speeded motor response to infrequent target gratings at the attended location that were slightly shorter than the rest.

2. Methods

2.1. Stimuli

Stimuli consisted of vertically oriented rectangular gratings ($5.0 \times 4.0°$ of visual angle) flashed (100 ms) one at a time in rapid (ISI = 250–330 ms, rectangular distribution) sequence on a video monitor (Fig. 1). The gratings were constructed of vertically orienting black and white stripes (contrast 100% — Michelson fraction) having a spatial frequency of approximately 2.0 cyc deg^{-1} of visual angle, and a space-averaged luminance equivalent to a gray background on the video monitor. The gratings were presented to locations in the upper visual field at eccentricities of 5.0° (to center) in the left and right visual hemi-fields. The location in each hemifield that the stimuli could appear at were continuously demarcated by a small square (0.25°). Stimulus durations were 100 ms, and the stimuli were presented to the left or right location in a random sequence. A random 25% of the gratings were slightly shorter and these were designated 'targets' when they occurred in the attended hemifield, while the other 75% of the gratings were designated 'standard' stimuli (i.e. non-targets). The height of the infrequent target gratings was between 10 and 20% shorted than the standards, and was adjusted for each subject to maintain performance between 70 and 90% accuracy.

2.2. Subjects

Right-handed male subjects ($N = 11$; mean age 25 ± 4 years) volunteered for the study. Of the 11 subject participating in the study, nine completed all six PET scans (two in each of the three conditions described below) while two subjects completed only one scan in each of the three conditions (the data from all 11 were included in the PET analyses). The subjects participated in two separate recording sessions on separate days, one for PET and one for ERP recording (one subject was excluded from the dipole analysis due to artifacts at some electrodes). Informed consent was obtained from each volunteer. The experiments complied with the Helsinki Declaration and with the requirements of the Human Subjects Review Committees at the authors' universities. Anatomical magnetic resonance imaging (MRI) scans were obtained in a third session using a fast gradient-echo three-dimensional sequence on a Siemens Vision MR scanner. The image resolution was 1 mm in the transverse plane and 1.25 mm in the axial plane.

2.3. Eye monitoring

During the task, the subjects were instructed to maintain ocular fixation on a central square (0.1°) on the screen. Eye position was monitored during the PET sessions using an infrared zoom lens video system, and during the ERP sessions using both electro-oculographic recording and infrared video zoom lens monitoring. Deviations of the eyes resulted in artifact rejection of individual trials or entire blocks in the ERPs, or entire blocks (i.e. one scan) in the PET sessions (where single trials could not be rejected).

2.4. Tasks

Three main task conditions were presented in separate counterbalanced blocks. These were: (i) covertly attend-left, ignore the right; (ii) covertly attend-right, ignore the left; and (iii) passively view the stimuli, all with fixation maintained on the fixation square. During the attend-left and attend-right conditions, the subjects were required to discriminate whether the stimuli in the attended location were tall or short. In response to the shorter target gratings they were required to press a button with the index finger of their right hand; no response was required to the taller standard stimuli in the attended locations, nor to the tall or short gratings in the unattended location. The subjects were instructed to press as rapidly and accurately as possible, and button presses earlier than 150 or later than 800 ms after stimulus onset were discarded. During the passive viewing conditions, the subjects were instructed merely to maintain fixation centrally, and not to attend to or respond to any of the stimuli.

2.5. PET methodology

In the PET session, a total of six bolus intravenous injections (1500 MBq each) of $15O$-butanol (half-life of 123 s) were administered (two in each of the three different conditions). Subjects were rigidly fixed in the scanner in a head holder, and viewed a suspended video monitor located above their chests as they lay in the scanner gantry. The scanner was a GE PC4096 Plus, which permitted 15 transverse slices to be acquired through the brain (6.5 cm center-to-center). Transmission scans for attenuation correction were performed with a Ge-68/Ga-68 rotating line source. The scanner specifications have been described in detail previously (Rota-Kops, Herzog, Schmid, Holte, & Feinendegen, 1990).

One minute prior to injection of the radiotracer, the subject was instructed to fixate their eyes on the fixation square and stimulus presentation began. Thirty seconds prior to injection the subject was given the task instructions for that run and told to begin the task (an arrow above fixation indicate attention should be directed to left or right). This permitted the subject's eye position to be monitored at the point of (and following) delivery of the attentional instructions, but after a baseline period of 30 s of ocular fixation when they did not know which task condition would be required. Following the injection, the data was acquired for a 40 s period that began when radiation counts in the head reached a threshold value indicating entry of the radiotracer into the brain.

The PET data were reconstructed following attenuation correction, and filtered using a 7 mm Hanning Filter (full width half maximum — FWHM). Given that radiation counts are proportional to regional cerebral blood flow (rCBF) when acquired in the manner used here (Herscovitch, 1994), no arterial sampling was employed, and the activity images were considered to be estimates of rCBF. Statistical Parametric Mapping (SPM96) was employed for image analysis (e.g. Friston, 1994). Each reconstructed PET scan was realigned to the MRI and reoriented along the bi-commissural line using a PET template in a standard stereotactic space (SPM96). A 15 mm FWHM Gaussian filter was applied to the data to compensate for inter-subject differences. Analysis of covariance (ANCOVA) was used to account for differences in global blood flow between subjects, and global cerebral blood flow was normalized to 50/100 ml min^{-1}.

T-statistics were then computed between pairs of conditions as follows: (1) attend-left vs. passive viewing; (2) attend-right vs. passive viewing; (3) attend-left vs. attend-right; and (4) attend-right vs. attend-left. The resulting t-statistic maps were converted to Z maps. Significant activations were identified as regions with Z scores $\geqslant 3.5$ and belonging to clusters of more than 100

Table 1
Brain areas showing increases in regional cerebral blood flow in comparisons of attention conditions to the passive viewing condition[a]

Contrast	Region	Side	x	y	z	Z score
Attend-right vs. passive	Fusiform gyrus	L	−36	−76	−16	5.15
	Anterior cingulate	L	−6	2	44	5.67
	Prefrontal cortex	R	34	30	10	4.8
	Prefrontal cortex	R	40	2	36	4.04
	Motor cortex	L	−50	−8	40	4.64
	Thalamus	L	−8	−16	2	4.48
	Cerebellum	R	36	−54	−32	4.77
Attend-left vs. passive	Fusiform gyrus	R	40	−68	−16	5.84
	Anterior cingulate	M	−6	4	44	4.35
	Prefrontal cortex	R	40	36	20	3.93
	Thalamus	R	6	−18	−12	4.04

[a] The x (left/right), y (anterior/posterior), and z (dorsal/ventral) coordinates refer to the standard stereotactic space of Talairach and Tournoux (1988). L, left hemisphere; and R, right hemisphere.

activated pixels ($2 \times 2 \times 2$ mm) for the comparisons to passive viewing. Within the ventral visual cortex, significant activations were identified as regions with Z scores $\geqslant 2.5$ and cluster sizes of 50 voxels for the comparison of attend-left to attend-right conditions (owing to the a priori hypotheses generated by our earlier studies Heinze et al., 1994; Mangun et al., 1997). That is, a more conservative criterion was established for regional activations not specifically predicted by the experimental hypothesis.

In the ERP session, EEG was recorded from 32 channels (0.16–64 Hz bandpass), digitized at 250 Hz, and stored for off-line analysis. Subjects wore tin electrodes mounted in an elastic electrode cap (Electrocap Int.); electrode impedances were maintained below 5 KΩ. The electrodes were approximately equally spaced across the scalp, and the precise locations were digitized in 3-D for each subject. During recording, the scalp electrodes were referenced to the right mastoid process. Following artifact rejection for eye movements, blinks, blocking, and movements artifacts, ERPs were separately calculated for the standard and target left and right stimuli. Dipole modeling was performed using the Brain Electric Source Analysis (BESA) method (e.g. Plendl et al., 1993). A three-shell spherical head model was used, and neuroelectric activity was modeled as point source dipoles. The BESA coordinates were converted to Talairach coordinates to relate the ERP to the PET data (e.g. Heinze et al., 1994). Scalp topographic mapping was performed using the spherical spline method in BESA (Version 2.2). Analysis of variance (ANOVA) was performed on electrodes sites T01 and T02 (lateral to O1 and O2 of the International 10–20 system) for the P1 and N1 components based on the prior literature. The ANOVA factors were: Visual Hemifield (left vs. right), Attention (attended vs. ignored), Hemisphere of Recording (left vs. right) and subjects.

3. Results

3.1. PET results

During the PET session, subjects detected the targets with a mean target detection rate was 75%. The corresponding mean reaction time was 467 ms. There was no significant difference for the left versus right hemifield targets. Thus, overall the subjects were accurate and fast in responding to the targets. No responses were made to targets presented in the unattended location.

Significant increases in regional cerebral blood flow were observed in several brain regions as a function visual spatial attention. These are listed in Table 1 for comparisons of the attention conditions to the passive viewing condition. Of particular importance to the present study were activations in the visual cortex. When subjects attended to the right visual hemi-field (versus passive viewing), there were significant activations in the left ventral and ventral–lateral occipital cortex. Whereas, when attention was directed to the left hemifield location (versus passive viewing), the activations were in the right occipital cortex. These included activations in the posterior fusiform gyrus, replicating our prior studies (e.g. Heinze et al., 1994; Mangun et al., 1997). The direct comparisons of the two attention conditions (attend-left vs. attend-right), which are matched for general arousal, primarily revealed significant activity in the ventral visual cortex in each hemisphere (Fig. 2 and Table 2). Thus, using unilateral, simple grating stimuli, attention-related activations in the contralateral ventral visual cortex were observed in regions very similar to those we observed using more complex stimuli and tasks in prior studies.

Activations in more anterior regions and frontal cortex were also observed (Table 1). For comparisons of focal attention (left or right) versus passive viewing, these included blood flow increases in the right prefron-

tal cortex (Brodmann's areas (BA) 45, 46), and the anterior cingulate gyrus (BA 24). Subcortical activations were seen in the contralateral thalamus and the cerebellum bilaterally. Blood flow decreases were shown in the left prefrontal region (BA 44, 45, 47), the occipital pole (BA 17/18), and the precuneus (BA 19, 7) (Table 3).

3.2. Event-related potential results

During the ERP session, subjects detected the targets with high accuracy. The mean target detection rate was 70%. The corresponding mean reaction time was 477 ms. There were no differences for accuracy or reaction times to targets in the left versus right visual hemifield. Errors in responding to the unattended side were not observed.

ERPs to the lateralized standard and target stimuli showed a pattern of voltage deflections (components) over posterior scalp. Only the data from the standard stimuli were evaluated and modeled since these more frequent events provided more trials and hence higher signal-to-noise ratios for modeling. The sensory-evoked components included the occipital CI component

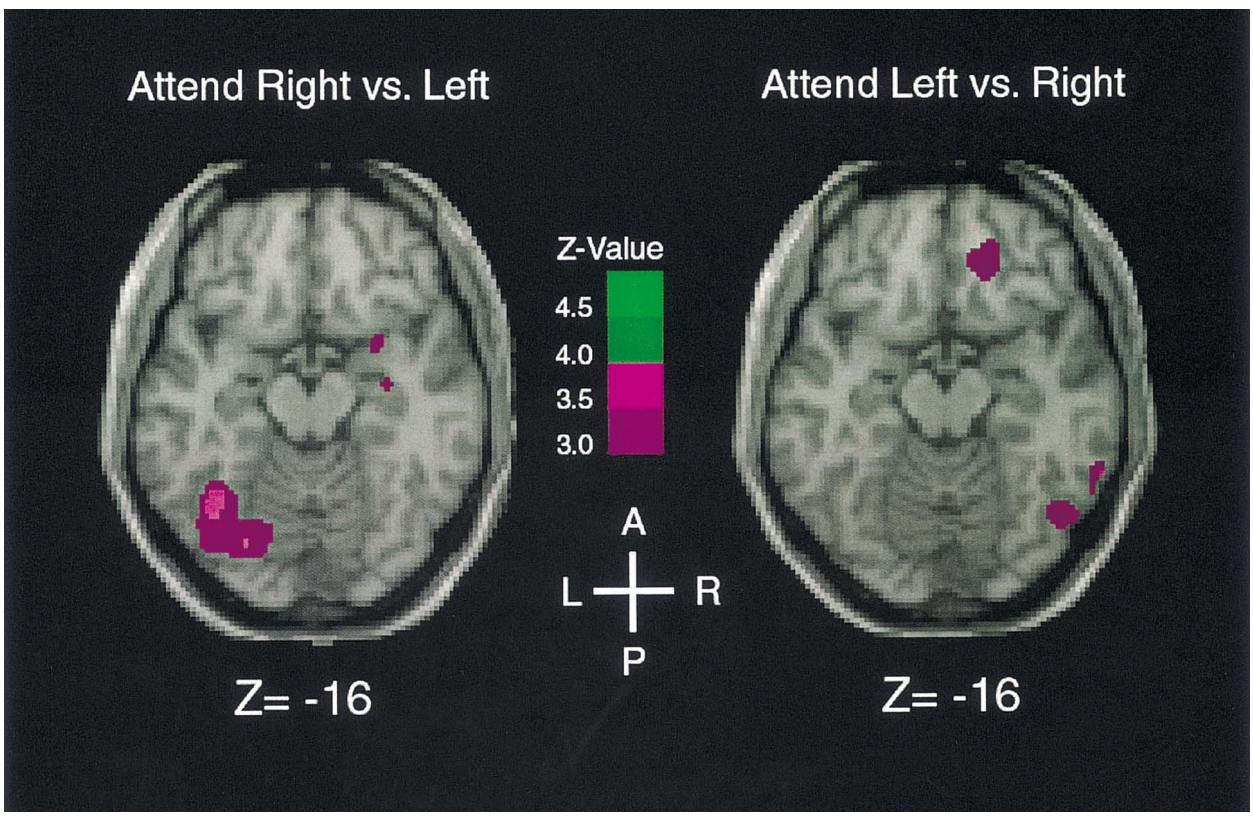

Fig. 2. Changes in regional cerebral blood flow with spatial attention. PET activations overlaid onto high-resolution structural MRI scans. Horizontal sections are shown at a Talairach Z of −16. Left brain is on the left of each figure. Attention to the right stimulus location (versus attending left) produced increases in blood flow in the contralateral left occipital cortex (left half of figure), while attention to the left stimulus location produced similar activations in the contralateral right hemisphere (right half of figure).

Table 2
Brain areas showing increases in regional cerebral blood flow in direct comparisons of the attend-left and attend-right conditions[a]

Contrast	Region	Side	*x*	*y*	*z*	*Z* score
Attend-right vs. attend-left	Posterior fusiform gyrus	L	−40	−62	−18	4.13
	Posterior fusiform gyrus	L	−26	−78	−10	4.18
	Anterior superior/middle temporal gyrus	R	42	10	−24	3.73
Attend-left vs. attend-right	Posterior fusiform gyrus/inferior occipital gyrus	R	46	−66	−14	3.46
	Inferior occipital/post inferior temporal gyrus	R	64	−50	−16	3.58
	Medial orbitofrontal cortex	R	18	43	−20	3.76

[a] The *x* (left/right), *y* (anterior/posterior), and *z* (dorsal/ventral) coordinates refer to the standard stereotactic space of Talairach and Tournoux (1988). L, left hemisphere; and R, right hemisphere.

Table 3
Brain areas showing decreases in regional cerebral blood flow in comparisons of passive viewing to attention conditions[a]

Contrast	Region	Side	*x*	*y*	*z*	*Z* score
Passive vs. attend-right	Occipital pole	L	−26	−98	−22	4.77
	Occipital pole	R	22	−96	−26	4.36
	Temporoparietal cortex	L	−42	−64	26	4.65
	Prefrontal cortex	L	−44	38	−12	4.34
	Precuneus cortex	M	−6	−64	4	4.32
	Prefrontal cortex	L	−24	64	10	4.2
	Prefrontal cortex	L	−14	34	40	4.06
	Prefrontal cortex	L	−54	22	0	3.84
Passive vs. attend-left	Occipital pole	R	36	−94	−24	4.6
	Temporal cortex	R	44	2	−20	3.92
	Precuneus	M	−4	−64	4	4.56
	Prefrontal cortex	L	−54	24	8	4.65

[a] The *x* (left/right), *y* (anterior/posterior), and *z* (dorsal/ventral) coordinates refer to the standard stereotactic space of Talairach and Tournoux (1988). L, left hemisphere; R, right hemisphere; and M, midline (less than 8 mm to the right or left of midline).

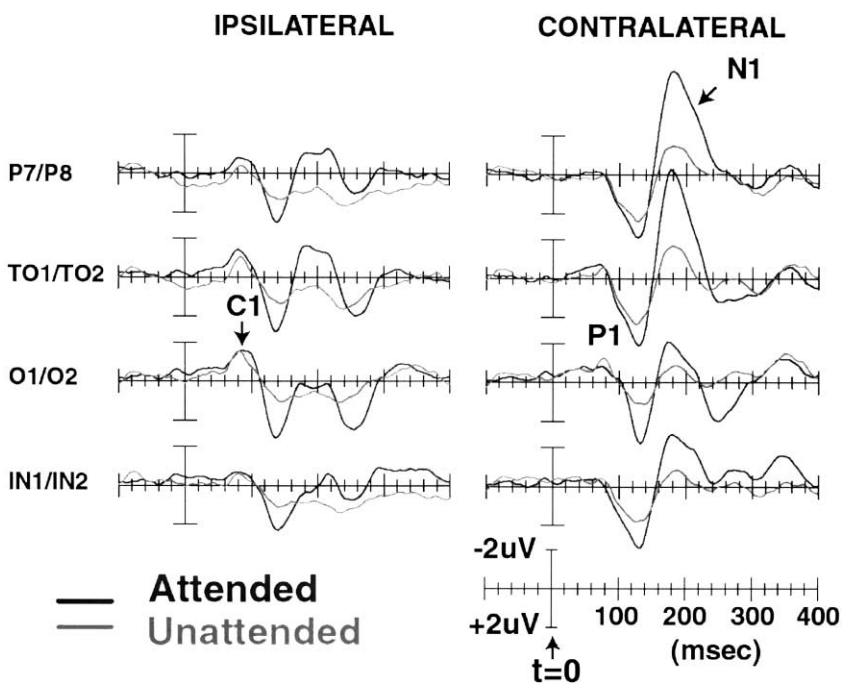

Fig. 3. Event-related potentials to the grating stimuli when attended and ignored. The ERPs were collapsed over the scalp sites contralateral and ipsilateral to the stimulus for ease of presentation. Thus, for example, contralateral occipital scalp sites (right half of figure) for attended stimuli were constructed by collapsing together the waveforms from the left occipital site O1 for attended right stimuli with the waveforms for attended left waveforms recorded from O2. The P1 and N1 components were modulated by attention over contralateral and ipsilateral sites (compare attended in solid to unattended in dashed). Positive voltage is plotted downward.

(sometimes denoted N70 or NP80 in the literature) presumed to be generated in striate cortex (50–90 ms latency — e.g. Clark & Hillyard, 1996; Martinez et al., 1999), as well as the P1 (70–130 ms latency — e.g. Van Voorhis & Hillyard, 1977; Eason, 1981) and the N1 (160–210 ms — e.g. Van Voorhis & Hillyard, 1977; Eason, 1981).

Significant amplitude modulations of some of these components were observed as a function of visual spatial attention (Fig. 3). Attention effects were first observed in the occipital P1 component. This was manifest statistically as a main effect of attention at lateral occipital sites TO1 and TO2 for mean amplitude measures in the window from 70–100 ms after stimulus onset ($F[1, 10] = 5.71$, $P < 0.038$), and also from 100–130 ms latency ($F[1, 11] = 5.30$, $P < 0.44$); there were no two-way interactions of the effect with visual field or hemisphere of recording for the P1. The later lateral occipital N1 component was also significantly modulated by attention at contralateral temporal–occipital

electrode sites (T01 and T02). This was manifest statistically as a three-way interaction of visual field × attention × hemisphere of recording that reflected that the attention effect on the N1 was highly contralateral ($F[1, 10] = 11.22$, $P < 0.01$, in the 160–190 ms window). The earlier C1 component did not show modulations by attention in this task. In general, these findings are consistent with numerous prior studies of visual spatial attention using ERPs (e.g. Mangun & Hillyard, 1988, 1990; see Mangun, 1995 for a review).

3.3. Integrated modeling

In order to investigate the relationship between attention effects in the ERPs and those in the PET activations, we asked two questions. First, could neuroelectric activity in the region of the PET-defined locations have generated the pattern of ERP effects recorded on the scalp? We investigated this question by 'seeding' model dipole sources to locations in visual cortex defined by our PET data but permitting dipole orientation and magnitude to vary. The ERP data that were modeled were the attention difference waves (attended–unattended) for the left and right visual field stimuli separately. We focused on the peak of the P1 in the 127–137 ms time window. Since in the PET data the attention effects are essentially collapsed over left and right stimuli by the block design and constraints of the analyses, we used the PET activations in visual cortex defined by the attend-left minus attend-right (and vice versa) contrasts as loci for seeding model dipoles. These comparisons contrast attention conditions that are equivalent in terms of non-specific arousal. Two types of seeding were performed, one in which a single dipole was placed in each hemisphere, at the PET-defined loci, and these loci were held constant while the dipole orientations and magnitudes were permitted to vary; we refer to these models as the 'seeded dipole models'. A second approach, we refer to as 'semi-seed models', involved placing one dipole in each hemisphere at the same PET-defined loci as indicated in the foregoing, and then holding location constant only for the dipole in the hemisphere contralateral to the hemifield of the stimulus. Hence, for example, in the attend-left condition, the contralateral right hemisphere dipole was held constant in the seeded location, but the ipsilateral dipole was permitted to vary in all parameters.

These same PET-defined activities were also used to address the second question, which was: How close would the correspondence be between unconstrained inverse models of the ERPs effects and the activity identified by PET? We investigated this by determining the 'best fit model' solutions and comparing these to the PET-defined loci. For the best fit models the dipoles were placed in the PET-defined loci as starting positions, but then all parameters (location, orientation, magnitude) were allowed to vary. Thus, in this case, only the number of dipoles and their starting positions were constrained. In each modeling exercise, the final model solution was considered to be that with the lowest residual difference (residual variance) between the recorded data and the model data (given the constraints for each model type indicated above).

A spherical, three-shell head model was used, and the coordinates of the PET activations were transformed into the spherical model using a linear transformation as specified in the BESA software package. Thereupon, model dipolar electric sources (point sources) were placed in the model head at the center of the PET activations and modeling was performed as described in the foregoing.

For the seeded dipole model, sources located in the PET-defined loci in ventral visual cortex (posterior fusiform gyrus) provided fairly good accounts of the ERP attention effects in the latency range of the P1 component (Table 4). The residual variance (RV) between model and recorded data was less than 6.5% for attend-left (vs. attend-right) and attend-right (vs. at-

Table 4
Dipole fitting results for ERPs when dipoles were constrained (full seed), partially constrained (semi seed) and unconstrained (best fit) by PET activation foci[a]

Condition	Best fit				Semi seed				Full seed			
	rv (%)	*X*	*y*	*z*	rv (%)	*x*	*y*	*z*	rv (%)	*x*	*y*	*z*
Attend-left vs. attend-right for left stim.												
Right hemisphere	**1.85**	38	−76	−25	**2.37**	*46*	*−66*	*−14*	**6.49**	*46*	*−66*	*−14*
Left hemisphere		−28	−49	−22		*−36*	*−48*	*−26*		*−26*	*−78*	*−10*
Attend-right vs. attend-left for right stim.												
Right hemisphere	**1.76**	33	−45	−7	**1.92**	36	*−44*	*−7*	**6.07**	*46*	*−66*	*−14*
Left hemisphere		−22	−79	−3		*−26*	*−78*	*−10*		*−26*	*−78*	*−10*

[a] Coordinates in italics represent fixed dipole locations based on the coordinates of PET activations. 'full seed' reflects fixing the locations of both left and right hemisphere dipoles to PET activations and permitting orientation and magnitude to vary. The 'semi seed' fixed the position of the contralateral dipole only, permitting the ipsilateral to vary in location to find lowest residual variance models. 'Best fit' reflects no constraints on the two dipoles.

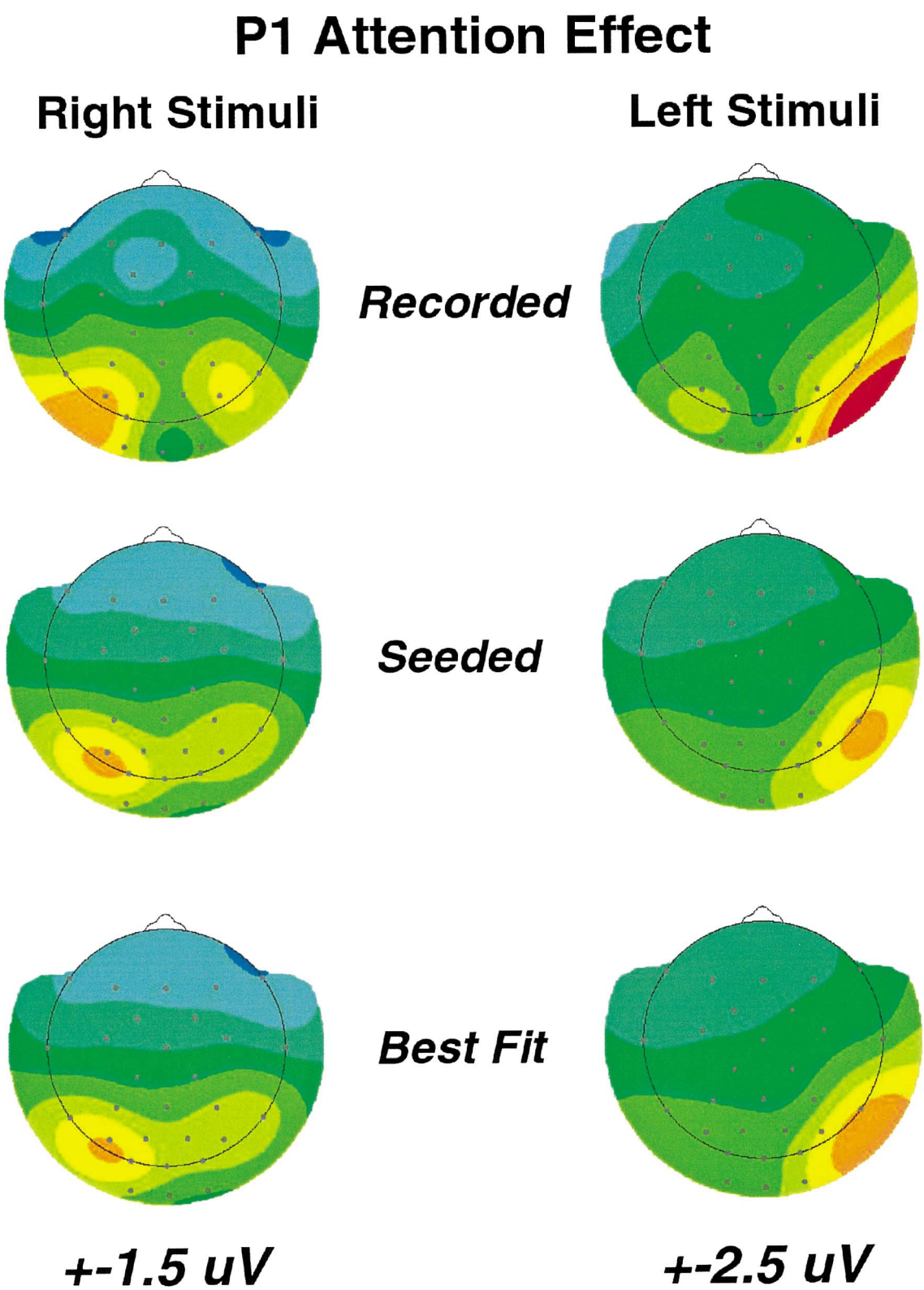

Fig. 4. Topographic voltage maps for recorded and modeled attention effects. Left maps are for RIGHT stimuli (and models of right stimuli) and right maps are for LEFT stimuli (and models for left stimuli). Top: Topographic voltage maps near the peak of the P1 component (127–137 ms latency) for the recorded data. Middle: The fully seeded dipole models, where one dipole in each hemisphere was placed at the loci of the contralateral PET activity. These dipoles were locked in place but permitted to vary in orientation and eccentricity (RV = 6.49 and 6.07% for left and right stimuli, respectively). Note that the semi-seed maps are not shown in the figure — see Table 4. Bottom: Best fit model in which dipoles were permitted to vary in all parameters (RV = 1.85 and 1.76% for left and right stimuli, respectively). The scales for the right maps varied from -2.5 (blue) to $+2.5$ uV (red). The scales for the left maps varied from -1.5 (blue) to $+1.5$ uV (red).

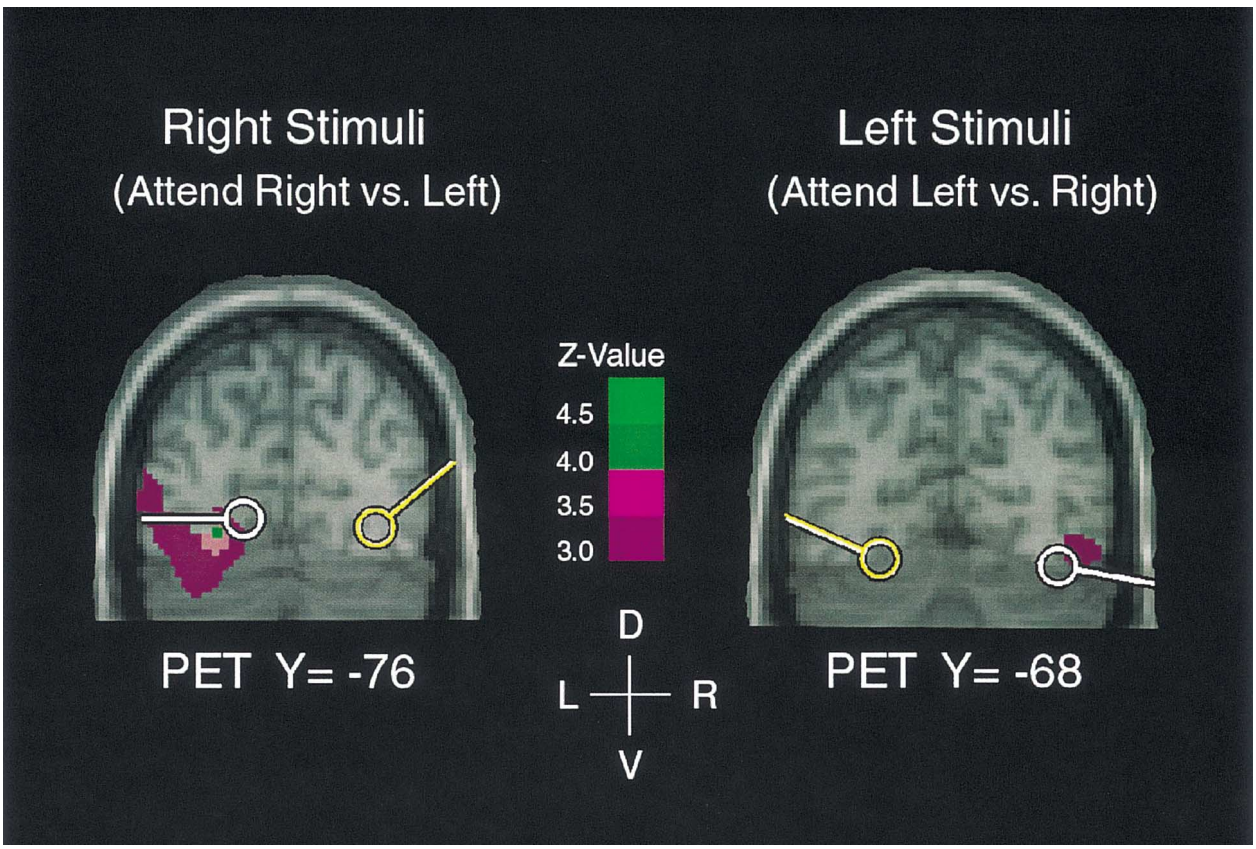

Fig. 5. Best fit dipoles compared to PET activations overlaid structural MRI scans. Coronal sections at the indicated Talairach *Y* coordinate. Increases in blood flow in visual cortex can be seen in the hemisphere contralateral to the direction of attention. The best fit dipoles are indicated as circles (the center of which is the location of the dipole in *X* and *Z* coordinates; the *Y* coordinates of the best fit dipoles and PET maxima differ in the figure in order to show the PET maxima (Table 4). The orientation of the dipoles are given by the bar attached to each circle. The white dipoles indicate the contralateral dipoles (e.g. the right hemisphere dipole solution for the attention effects on the left stimuli). Note the close correspondence between the dipole locations and the PET maxima in the hemispheres contralateral to the stimuli.

tend-left). For the semi-seed model where the location of the contralateral dipole but not ipsilateral dipole was fixed, a lower residual variance model was obtained (RV $< 2.5\%$). Finally, for the best fit models, where the dipoles were unconstrained in each visual cortex, the residual variance of the models were lowest, being less than 1.9% in each model. Fig. 4 shows the topographic maps for the recorded data, and the seeded and best fit dipole models. Outside the time range of the P1, dipoles in this regions provided poorer fits to the real data. Thus, the dipole models for the earliest attention effects in visual cortex, around the peak of the occipital P1 component of the ERP, were well accounted for in each of the dipole models. However, in the case of the best fit models, the loci of the model dipoles were found to be slightly medial, posterior and ventral to the PET-defined maxima in the right hemisphere for attention to the left, and slightly more dorsal in the left hemisphere for attention to the right. In each case for the best fit dipoles, the model dipoles were closest to PET-defined maxima in the hemisphere contralateral to the attended stimulus. This was specially true for the attend-right versus attend-left comparison for right stimuli in the left hemisphere where the best fit dipole moved only slightly more dorsal (Fig. 5).

4. Discussion

This study combined electrophysiology and functional neuroimaging to investigate the neural mechanisms of visual spatial attention. The findings provide additional evidence in support of the idea that visual spatial attention involves the modulations of incoming sensory signals in human visual cortex. This evidence includes observations of attention-related changes in regional cerebral blood flow in visual cortex in conjunction with changes in the amplitudes of sensory-evoked responses in the ERPs at latencies consistent with processing early in extrastriate cortex (70–130 ms). These findings replicate our prior work using combined ERP and PET or fMRI measures (Heinze et al., 1994; Mangun et al., 1997, 1998) and are consistent with more recent studies using combined methodological ap-

proaches (e.g. Gratton, 1997; Woldorff et al., 1997; Martinez et al., 1999, this issue; Woldorff, Matzke, Zamarripa, & Fox, 1999), as well as several studies investigating visual spatial attention using functional imaging alone (e.g. Tootell et al., 1998; Somers et al., 1999).

More specifically, the results demonstrate that attention-related activations in the ventral visual cortex in and around the posterior fusiform gyrus do not depend upon higher-order form discrimination processes for attended stimuli, nor upon the requirement that subjects engage in complex pattern matching operations. This is because attentional activations in this region were obtained in the present study for simple vertical grating targets, only the height of which was to be discriminated. Further, since the stimuli were presented unilaterally, the attention effects in and around the posterior fusiform are not the result of competition between simultaneously presented targets and distractors (e.g. Desimone & Duncan, 1995; Kastner & Ungerleider, 2000), as might have been the case in our earlier studies Heinze et al., 1994; Mangun et al., 1997; Mangun et al., 1998). Thus, the present PET results provide further evidence that the attention-related neural activity in the ventral, extrastriate visual cortex bears functional similarity to that reflected in the P1 component of the ERPs, supporting the idea that early in vision, spatial attention can modulate visual information processing based on location information (e.g. Hillyard & Münte, 1984; Mangun, 1995). The present data also fit well with our prior report of activations in posterior fusiform gyrus when spatial attention was allocated to lateralized targets in order to either discriminate pairs of nonsense symbols or merely detect a small dot (luminance target) that might be present within the confines of the flashed symbols which were not distracters (Mangun et al., 1997). This does not argue against the idea that attention can act on object-based representations (e.g. Roelfsema, Lamme, & Spekreijse, 1998; O'Craven, Downing, & Kanwisher, 1999), but rather adds to the evidence that spatial location is also a powerful cue for early attentional modulation in vision. Precisely which mechanism (spatial or object) first modulates input processing cannot be answered based on the present data, however, activations related to object-based attention in recent studies were found to be located more anteriorly in the fusiform gyrus and in the parahippocampal cortex in regions that were specifically coding object representations (e.g. O'Craven et al., 1999).

The argument that the PET activations in ventral visual areas are related to attentional modulations of sensory input processing (as opposed to longer-latency reafferent activation of extrastriate cortex) is based on the corresponding electrical recordings. The ERPs observed to the same grating stimuli while the subjects performed the identical height discrimination task showed attentional modulations (attended vs. unattended stimuli) with latencies as short as 70–100 ms after the onset of the stimuli (onset of the P1 component). This latency range is consistent with input processing in extrastriate cortex (e.g. Robinson & Rugg, 1988). Dipole modeling showed that the attention-related activity in visual cortex identified by the PET measures occurred in close proximity to the best fit dipole models of the ERP attention effects. This was especially true for the dipole locations and PET activations in the hemisphere contralateral to the stimuli (Fig. 5). Our findings fit well with other dipole models of visual spatial attention effects (Woldorff et al., 1997; Martinez et al., 1999, this issue), however, the localizations are not precisely the same. This is likely due to differences in the stimuli used across the studies. While we used upper field stimuli in the present study, Woldorff et al., 1997 used lower hemifield stimuli, and Martinez et al. used stimuli that straddled the horizontal meridian. Since upper and lower visual field representations map to ventral and dorsal visual cortical regions, respectively, (e.g. Sereno et al., 1995; Woldorff et al., 1997) any difference among these studies of spatial attention might be attributable to differences in the retinotopic mapping of the stimuli within visual cortex. As well, the strategies used among the foregoing studies for dipole modeling differed slightly, although all used equivalent current dipoles in a spherical head model using the BESA algorithm.

The results of the present study also address the question of which brain areas are involved in top-down attention control (e.g. Posner & Petersen, 1990). Brain regions presumably involved in attentional control were also identified, including the anterior cingulate cortex and prefrontal cortex. These findings are in line with prior reports in similar tasks (e.g. Corbetta, Miezin, Shulman, & Petersen, 1993; Heinze et al., 1994). However, no activations were observed in the parietal cortex, which might have been expected given prior neuroimaging studies (e.g. Nobre et al., 1997; Corbetta, 1998; Gitelman et al., 1999), and a long history of attentional deficits following parietal damage (see, Mesulam, 1999, for a review). However, prior studies using sustained spatial attention have similarly failed to observed attention-related activity in parietal cortex (e.g. Heinze et al., 1994; Mangun et al., 1997), whereas those involving shifts of attention have typically reported parietal activations (e.g. Corbetta, Shulman, Miezin, & Petersen, 1995). Indeed, studies that used event-related fMRI methods to disentangle attentional orienting (e.g. to a cue) from subsequent target processing have shown that parietal cortex is most activated to attention-directing cues that trigger shifts of attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000). In

studies such as the present, that involve focused attention across blocks of trials rather than trial-by-trial attentional shifts, changes in regional cerebral blood flow in parietal cortex may be too small to be detected in many circumstances (Vandenberghe et al., 2000).

4.1. Summary

Taken together, the ERP and PET data reinforce the concept of a spatially-restricted attentional 'spotlight' that acts to relatively facilitate the processing of events occurring within the attended spatial zone. Thus, at this stage of visual processing, occurring early in extrastriate visual cortex, the effects of simple spatial attention can be likened to a spotlight that facilitates the processing of stimuli falling within the confines of the attended zone of visual space. We based this on the evidence here that spatial attention to simple, isolated stimuli requiring an elementary discrimination are sufficient to engage this early attentional mechanism in visual cortex. The evidence from integrated modeling strongly suggests that these attentional influences occur initially on the stimulus inputs, and therefore are likely preset as tonic, top-down modulatory effects of attention on early visual processing (Martínez et al., 1999).

Acknowledgements

This research was supported by grants to H.J.H. from the DFG and to G.R.M. from the NIMH (MH55714), the U.S. Army Research Office, and the Human Frontier Science Program.

References

Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the 'spotlight' of visual attention. *Nature Neuroscience*, *2*, 370–374.

Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects extrastriate but not striate components of the visual evoked potential. *Journal of Cognitive Neuroscience*, *8*, 387–402.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences*, *95*, 831–838.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science*, *248*, 1556–1559.

Corbetta, M., Miezin, F., Shulman, G., & Petersen, S. (1993). A PET study of visuospatial attention. *Journal of Neuroscience*, *13*, 1202–1226.

Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.

Eason, R. G. (1981). Visual evoked potential correlates of early neural filtering during selective attention. *Bulletin of the Psychonomic Society*, *18*, 203–206.

Friston, K. J. (1994). Statistical parametric mapping. In: Thatcher et al. (Eds.), Functional neuroimaging: technical foundations, Academic Press, San Diego, pp. 79–91.

Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S., Kim, Y. H., Meyer, J. R., & Mesulam, M. (1999). A large-scale distributed network for covert spatial attention: further anatomical delineation based on stringent behavioural and cognitive controls. *Brain*, *122*, 1093–1106.

Gratton, G. (1997). Attention and probability effects in the human occipital cortex: an optical imaging study. *Neuroreport*, *8*, 1749–1753.

Handy, T. C., & Mangun, G. R. (2000). Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Perception and Psychophysics*, *62*, 175–186.

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., Gös, A., Johannes, S., Scherg, M., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of spatial selective attention in humans. *Nature*, *392*, 543–546.

Herscovitch, P. (1994). Radiotracer techniques for functional neuroimaging with positron emission tomography. In R. Thatcher, M. Hallet, T. Zeffiro, E. John, & M. Huerta, *Functional neuroimaging: technical foundations* (pp. 29–46). San Diego: Academic Press.

Hillyard, S. A., & Münte, T. F. (1984). Selective attention to color and location: an analysis with event-related brain potentials. *Perception and Psychophysics*, *36*, 185–198.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.

Kanwisher, N., & Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Reviews Neuroscience*, *1*, 91–100.

Kastner, S., & Ungerleider, L. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 887–904.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2 and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*, 24–42.

Mangun, G. R. (1995). Neural mechanisms of visual selective attention in humans. *Psychophysiology*, *32*, 4–18.

Mangun, G. R., & Buck, L. (1998). Sustained visual spatial attention produces costs and benefits in reaction time and evoked neural activity. *Neuropsychologia*, *36*, 189–200.

Mangun, G. R., & Hillyard, S. A. (1988). Spatial gradients of visual attention: behavioral and electrophysiological evidence. *Electroencephalography and Clinical Neurophysiology*, *70*, 417–428.

Mangun, G. R., & Hillyard, S. A. (1990). Allocation of visual attention to spatial locations: tradeoff functions for event-related brain potentials and detection performance. *Perception and Psychophysics*, *47*, 532–550.

Mangun, G. R., & Hillyard, S. A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 1057–1074.

Mangun, G. R., Hopfinger, J., Kussmaul, C., Fletcher, E., & Heinze, H. J. (1997). Covariations in ERP and PET measures of spatial selective attention in human extrastriate cortex. *Human Brain Mapping*, *5*, 273–279.

Mangun, G. R., Buonocore, M., Girelli, M., & Jha, A. P. (1998). ERP and fMRI measures of visual spatial selective attention. *Human Brain Mapping*, *6*, 383–389.

Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., Heinze, H. J., & Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*, 364–369.

Martínez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001). Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research*, *41*, 1437–1457.

McAdams, C. J., & Maunsell, J. H. R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience*, *19*, 431–441.

Mesulam, M. M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London — Series B: Biological Sciences*, *354*, 1325–1346.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*, 782–784.

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*, 909–919.

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron-emission tomography. *Brain*, *120*, 515–533.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). FMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584–587.

Plendl, H., Paulus, W., Roberts, I. G., Botzel, K., Towell, A., Pitman, J. R., Scherg, M., & Halliday, A. M. (1993). The time course and location of cerebral evoked activity associated with the processing of color stimuli in man. *Neuroscience Letters*, *150*, 9–12.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas v2 and v4. *Journal of Neuroscience*, *19*, 1736–1753.

Robinson, D., & Rugg, M. (1988). Latencies of visually responsive neurons in various regions of the rhesus monkey brain and their relationship to human visual responses. *Biological Psychology*, *26*, 111–116.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, *395*, 376–381.

Rota-Kops, E., Herzog, H., Schmid, A., Holte, S., & Feinendegen, L. E. (1990). Performance characteristics of an eight-ring whole body PET scanner. *Journal of Computer Assisted Tomography*, *14*, 437–445.

Sengpiel, F., & Huebener, M. (1999). Visual attention: spotlight on the primary visual cortex. *Current Biology*, *9*, 318–321.

Sereno, M., Dale, A., Reppas, J., Kwong, K., Belliveau, J., Brady, B., & Tootell, R. (1995). Borders of multiple visual areas in humans revealed by functional MRI. *Science*, *268*, 889–893.

Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. H. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences*, *96*, 1663–1668.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.

Tootell, R. B., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., & Dale, A. M. (1998). The retinotopy of visual spatial attention. *Neuron*, *21*, 1409–1422.

Vandenberghe, R., Dupont, P., De Bruyn, B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1996). The influence of stimulus location on the brain activation pattern in detection and orientation discrimination. A PET study of visual attention. *Brain*, *119*, 1263–1276.

Vandenberghe, R., Duncan, J., Dupont, P., Ward, R., Poline, J. B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1997). Attention to one or two features in left or right visual field: a positron emission tomography study. *Journal of Neuroscience*, *17*, 3739–3750.

Vandenberghe, R., Duncan, J., Arnell, K. M., Bishop, S. J., Herrod, N. J., Owen, A. M., Minhas, P. S., Dupont, P., Pickard, J. D., & Orban, G. A. (2000). Maintaining and shifting attention within left or right hemifield. *Cerebral Cortex*, *10*, 706–713.

Vanduffel, W., Tootell, R., & Orban, G. (2000). Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cerebral Cortex*, *10*, 109–126.

Van Voorhis, S. T., & Hillyard, S. A. (1977). Visual evoked potentials and selective attention to points in space. *Perception and Psychophysics*, *22*, 54–62.

Woldorff, M., Fox, P., Matzke, M., Lancaster, J., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J., Martin, C., & Jerabeck, P. (1997). Retinotopic organization of the early visual-spatial attention effects as revealed by PET and ERPs. *Human Brain Mapping*, *5*, 280–286.

Woldorff, M. G., Matzke, M., Zamarripa, F., & Fox, P. T. (1999). Hemodynamic and electrophysiological study of the role of the anterior cingulate in target-related processing and selection for action. *Human Brain Mapping*, *8*, 121–127.

Worden, M., & Schneider, W. (1996). Visuospatial attentional selection examined with functional magnetic resonance imaging. *Society for Neuroscience Abstracts*, *22*, 1856.